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## Connectivity needs for grassland arthropods

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# 1 Introduction

## 1.1 Context

The EU Biodiversity Strategy to 2030 addresses the continued decline of the conservation status of habitats and species in its Member States by planning to build a ‘truly coherent network of protected areas’. This network should legally protect at least 30 % of the EU’s land area and should comprise a ‘Trans-European Nature Network’ (TEN-N; European Commission, 2020).

The TEN-N will be build based on the existing Natura 2000 network by integrating ecological corridors using Green Infrastructure landscape elements. The EU-wide strategy on Green infrastructure (GI) was adopted in 2013 and promotes investments to ensure that natural areas remain connected together, to restore the health of ecosystems and allow species to thrive across their entire natural habitat, in order to ensure their contribution in the delivery of ecosystem services (European Commission, 2013).

To ensure that GI elements are integrated in a way that indeed allows to reach the above goals, a knowledge basis is needed concerning the connectivity needs of species, with a priority for species listed on the Annexes of the Habitat Directive. Previously, Condé *et al.* (2017) proposed a list of species that 1) need connectivity for biological dispersion, regular movement and/or migration and 2) for which an implementation of a GI project developed by one of several Member States can be of relevance for their conservation, with a focus on connectivity needs across national boundaries. Based on this list, Van der Sluis & Bouwma (2018) made a further selection of emblematic species with strong needs for connectivity.

Dispersal of animals to neighbouring habitats will depend on various parameters, among which importantly the size and quality of the source habitat and the size of the source population (a large population will result in more long-distance dispersal events even if such events are relatively rare). Yet, while conservation and strengthening of existing habitats thus is key, ensuring minimal possibilities for dispersal is a prerequisite for connectivity. Identifying maximum dispersal distances, as well as clear barriers for dispersal, will aid the construction of a functional habitat network.

Both of the abovementioned studies covered a broad range of taxonomic groups, including amphibians, fishes, mammals, reptiles, vascular plants and arthropods. The assessment for insects was restricted to the Coleoptera (beetles), Odonata (dragonflies and damselflies) and Lepidoptera (moths and butterflies). Dispersal potential of members of this group was assessed based on three wide distance classes and it was concluded that nearly all insect species showed maximum dispersal distances within the smallest class (0-40 kms). Potential measures to improve connectivity were provided for the subset of six emblematic species.

## 1.2 Study aims

Here, we extend the work by Condé *et al.* (2017) and Van der Sluis & Bouwma (2018) by performing a more fine-scale assessment of (maximum) dispersal distances in relation to different functions the connectivity may have for survival of individuals and/or populations. We focus on arthropod species related to some extent to grassland habitats, as a proof-of-principle. Furthermore, for this set of species we summarize knowledge on potential dispersal barriers (e.g. unsuitable habitat patches, waterways or roads), in order to provide recommendations for potential measures to improve connectivity between habitat fragments per taxonomic order. Knowledge gaps are indicated to focus further study.

## 2 Methods

### 2.1 Species selection

The current analysis was restricted to arthropod species occurring on either Annex II or IV of the Habitats Directive. A further selection was then based on Halada *et al.* (2021) who provide an ecological grouping of the Habitat's directive's habitats and species, including a database indicating per species its dependency on different broad habitat types. We selected all arthropod species for which grasslands were scored at least as "occasional habitat". This includes natural and semi-natural grasslands, but not intensive agricultural grasslands.

This resulted in a final list of 75 arthropod species used in the current study, of which 42 Lepidoptera (butterflies and moths), 12 Coleoptera (beetles), 10 Odonata (dragonflies and damselflies), 10 Orthoptera (grasshoppers and crickets) and one Mantodea (mantid). A full list of these 75 taxa is presented in Annex 1.

### 2.2 Definition of connectivity needs

Here, we focus on connectivity needs at the landscape scale, i.e. between habitat patches within a landscape (county, region or province level). This excludes shifts in distribution areas due to e.g. climate change; which will in practice often be a stepwise process acting at landscape scale). This focus provides the best link to the relevant ecological requirements for detection and prioritization of connectivity improvements within the TEN-N.

At the landscape scale, a given species may show different connectivity needs in relation to different types of dispersal behaviour. In their description of connectivity corridors, Van der Sluis, Bloemmen & Bouwma (2004) differentiate three functions of connectivity: commuting (regular movement between resting/breeding sites and foraging areas), migration (annual movement from breeding grounds to e.g. wintering grounds and/or vice versa) and dispersal (one-way movement for the purpose of immigration towards a different population or the colonization of new sites). Here we use a slightly adjusted framework of four functions, by splitting the "dispersal" function into a function for genetic exchange among populations and a function for (re)colonization of empty habitat patches. This results in the following four functions:

- 1) **Trans-habitat commuting.** This comprises daily movement between breeding/resting habitats and foraging habitat. Only relevant in certain species. Examples are damselflies resting at the water site but moving into grassland for foraging.
- 2) **Trans-habitat migration.** This comprises seasonal or annual movement between resting/breeding sites and foraging areas. Only relevant in certain species. Examples are certain butterflies that show long-distance southward migration for overwintering.
- 3) **Genetic exchange.** Regular immigration of new individuals into different populations is relevant for nearly all species, including insects. This is especially important when populations are small due to e.g. habitat fragmentation, in order to compensate for potential loss of genetic diversity. Such immigration events can be successfully performed by either male or female individuals, as long as individuals are able to be involved in future reproduction. Population genetic models assume a necessity of at least one immigrant per population per generation. In practice, dispersal barriers such as unsuitable habitat patches or infrastructure may therefore often result in problematic restriction of genetic exchange. Note that while evidence for limited genetic exchange beyond a certain distance indicates dispersal limitation, evidence for functional genetic exchange between two habitat patches does not mean that the distance between the patches is covered in one

dispersal event. Functional exchange may also be reached via stepwise dispersal via habitat elements located in between the studied patches.

- 4) **(Re-)colonization.** Immigration of new individuals into a habitat patch that was (temporarily) unoccupied by the species. (Re)colonization allows for a functional meta-population in which subpopulations re-establish after local extinction. Successful establishment can rely on occasional long-distance dispersal events, but requires the arrival of both a male and female reproductive individual (which may show different dispersal capacities).

### 2.3 Habitat cross-dependencies

In the current study we focus on needs for connectivity between patches of grassland habitat. We considered such connectivity as relevant for all species with respect to function 3 (genetic exchange) and 4 (colonization). Trans-habitat commuting and migration (function 1 and 2) are only relevant in some species using different habitats in different stages of their life cycle, while others can complete their life cycle entirely within a grassland patch (assuming the patch is of sufficient size and quality). Therefore, for each species we evaluated its cross-dependency on multiple habitat types, and if so, indicated between which habitat types connectivity should be realized. Again, the habitat/species database by Halada *et al.* (2021) was used as a basis. Unknowns were evaluated based on a combination of expert knowledge and literature study.

### 2.4 Assessment of distances and barriers for dispersal

Dispersal capacities were evaluated for each species based on a literature scan in Google Scholar using the species name and “dispers\*” as key words. In case not hits were found, the search was repeated at genus, family or eventually order level. Per connectivity function (see 2.2.) dispersal capacity was quantified as much as possible for each species by defining a maximum dispersal distance. Typically, dispersal kernels of arthropods show a strong decline at low distances followed by a long tail of occasional long-distance dispersal events. For the current study, maximum distances for genetic exchange were based on either evidence from population genetic analyses (if available) or based on dispersal kernels estimated by mark-release-recapture (MRR) or telemetry approaches, using the distance below which 95 % of the recorded dispersal events as a cut-off. Maximum distance for colonization was based on the largest distance reported in the literature for a single individual of the species (i.e. occasional long-distance dispersal events).

As the selected list of species did not include any migratory species showing long-distance migration between breeding and overwintering grounds, dispersal capacity for commuting and migration were lumped as ‘trans-habitat movement’. Maximum dispersal distances were given for this function where relevant (for species showing habitat cross-dependency).

While occasional dispersal of insect eggs and larvae has been reported and may contribute to colonization of distant habitat patches, this is thought to comprise a negligible proportion of dispersal events (see e.g. Angelibert and Giani 2003) and unlikely sufficient to reach functional connectivity. Here, we therefore focus on dispersal of either juvenile or adult individuals of the imago life-stage dispersing either by flight (if functional wings are present), jumping or running. Presence of functional wings often highly enhances dispersal capacity and was therefore recorded for each species.

The same literature scan was also used to retrieve information on the relevance of four types of infrastructure (waterways, railroads, roads and other) as barriers for dispersal. Per category, the role as barrier was scored as either “Yes”, “Potentially”, “No” or “Unknown”.

## **2.5 Potential measures for improvement of connectivity**

Here, we restrict to broad recommendations per order, based on collected knowledge on dispersal distances and habitat dependency. Types of corridors are suggested, based on the framework as described by Van der Sluis, Bloemmen & Bouwma (2004): linear corridors, linear corridors with nodes or stepping stones. A more detailed description of habitat structure of corridors per species will require further study (but see Van der Sluis & Bouwma (2018) for examples for a few emblematic species).

## 3 Results

### 3.1 Data availability

Availability of knowledge on dispersal behaviour in general, and dispersal distances in particular, varied widely between arthropod orders and among species within orders. Furthermore, various methodologies are available for assessment of dispersal distances, which all have their own benefits and pitfalls. To some extent different methods have been applied for different species. Only a few more well-known and widespread species have been studied using multiple methods. Although caution is thus required when comparing distance values for different species, in this report we summarize the available knowledge while indicating by which method the presented values were gathered.

For arthropods, MRR studies are the most common tool used to estimate dispersal (Elek *et al.* 2014). In MRR, individuals are captured, marked e.g. by painting a coloured dot or code on their body which allows individual recognition upon recapture and then released again. When the same individual is recaptured at a different site, a dispersal event is recorded, with a given minimum distance. By capturing animals at multiple sites with varying pairwise distances, incidence of dispersal over a range of distance classes can be estimated, which can then be used to model dispersal kernels (Jopp & Reuter 2005). Compared to other methods, such as population genetic analyses or telemetry, MRR-based results tend to give relatively low dispersal estimates, due to underestimation of occasional long-distance dispersal events (function 4; as such individuals disperse out of the study area and are not recaptured). It does however give a good indication of dispersal distances of the majority of individuals in a population, relevant for trans-habitat movement (function 1 and 2) and to some extent potential for genetic exchange (function 3). Yet, some studies are characterised by relatively low recapture rates, limited observation frequencies and/or short time scales, which restricts possibilities for generalization at species level.

Telemetry studies can yield better insights in long-distance dispersal events in case sufficient individuals are followed, yet has so far only rarely been used for insects as many species are too small to attach a transmitter without severely limiting its movement. One exception is the stag beetle (*Lucanus cervus*), which is relatively large and robust. For this species multiple telemetry studies have been performed in different parts of its distribution area in Europe (see 3.2.3).

Population genetic studies can give valuable insights in minimum or maximum distances over which genetic exchange can still occur to an extent that prevents genetic erosion, especially in case pairwise genetic distances have been measured for larger numbers of population pairs with a range of geographical distances. Yet, due to relatively high costs (at least in the past) and a lack of marker availability, this type of study has been conducted so far for only a handful of the species included in this report. Population genetic studies are less relevant to study potential for recolonization of distant habitat patches via occasional long-distance dispersal or recurring trans-habitat movement during the life cycle of a single generation.

### 3.2 Dispersal capacities per order

Available knowledge on dispersal capacities per species was summarized in a table per arthropod order, available as a separate excel database ("**Arthropod connectivity tables\_v1.0.xlsx**", Annex 2). Below, we briefly summarize the status of available knowledge per order.

Each table includes an indication per species of habitat cross-dependency, to assess the relevance of trans-habitat movement. Underlying details on the extent of preference for grassland and habitats used for different purposes (foraging and breeding) are specified in a separate worksheet in Annex 2.

### 3.2.1 Odonata

The Odonata consist of two ecologically different suborders: the Anisoptera or dragonflies and the Zygoptera or damselflies. Both groups show a clear habitat cross-dependency, in which freshwater habitats are required for breeding and grasslands are used for foraging. Yet the groups differ in time spent per habitat type. Anisoptera imagos usually spend at least part of their life away from their natal pond (Corbet *et al.* 2006). Males usually leave the water area to mature and forage but may move back and forth to the water, while females of most species only come to the water to breed (Corbet *et al.* 2006). Zygoptera are more strongly connected to freshwater shorelines and only disperse into grassland for small distances for foraging (e.g. Landmann *et al.* 2021).

Corbet *et al.* (2006) reported a clear difference in dispersal capacity between both groups, with Anisoptera showing a rather high dispersal power and Zygoptera showing a rather restricted dispersal. This general difference may relate to differences in body size, in particular wing span ratio, with larger species showing longer dispersal distances (Dolny *et al.* 2021). Swaegers *et al.* (2014) indicate a relation between dispersal capacity, measured as wing span ratio, and phylogeny. Hof *et al.* (2006) stress a difference between lotic species (preference for running water) and lentic species (preference for standing water) with lotic species generally showing smaller ranges. While such relations will especially hold for average dispersal distances per species, reported maximum dispersal distances strongly differ between species even within suborders.

As shown in the table in Annex 2, Odonata of both suborders are relatively good dispersers, with regular dispersal in the range of hundreds of meters but able to colonize patches located kilometers to (in some species) tens of kilometers away. Most available literature on dispersal of Zygoptera relates to the genus *Coenagrion* and in particular *C. mercuriale*. Swaegers *et al.* (2014) state that distances are likely similar for other members of the genus with similar body sizes. For that reason, we extrapolated colonization distance for *C. ornatum* based on values for its near relative *C. mercuriale*. Distances for genetic exchanges for Zygoptera and Anisoptera were extrapolated based on a study by Conrad *et al.* (1999) of seven Odonata species from various families including Coenagrionidae and Libellulidae.

Evidence for dispersal barriers is extremely sparse for Odonata. Most species are good fliers and likely can cross waterways at least to some extent, although the strong relation of Zygoptera with shoreline vegetation may limit their dispersal across larger bodies of water. In a MRR study for *Coenagrion hylas* along a 30km long river stretch Landmann *et al.* (2021) recorded river crossings at a site where the river was 25m wide, but not at other sections where the river was 100 to 250m wide. Purse *et al.* (2003) showed that dispersal was limited for *C. mercuriale* in case they needed to cross a row of shrubs. The same may be true for other Zygoptera although no evidence exists so far. No studies were found that report on the effects of roads or railroads on connectivity of Odonata.

### 3.2.2 Orthoptera

A wealth of papers has been produced on the ecology of European Orthoptera. This includes studies on their dispersal behaviour, summarized by Bruckhaus & Detzel (1999). Yet, Reinhardt *et al.* (2005) report doubts casted on their classification by later studies and provide a revised classification. Given the strong uncertainties, their index is very conservative and simply divides Orthoptera into three dispersal classes ranging from low mobility (1) to high mobility (3), without any further quantification of the distance range per class. All wingless species are grouped in class 1.

Furthermore, none of the species included in the current study, which are mostly relatively rare and show a very restricted distribution range, was included in the list of Reinhardt *et al.* (2005). In conclusion, quantitative data on dispersal of the Orthopteran species studied in this report are apparently absent. Any estimations currently must be extrapolated from related species with similar morphology and ecology.

The grassland Orthoptera listed on the Habitats Directive belong either to the Ensifera (crickets) or the Caelifera (grasshoppers).

Most included crickets are bush crickets (family *Tettigoniidae*). They vary in body size, but all are wingless ground-dispersers, limiting their dispersal distances and likely resulting in at least waterways being a hard barrier. Dorkova *et al.* (2005) assume a maximum colonization distance for the bush cricket *Pholidoptera transsylvanica* of 1 kilometer, based on data for related wingless bush crickets of similar size'. Given the assumed relevance of body size, this estimate cannot be readily translated to other members of the family, although dispersal for multiple kilometers is unlikely. For *P. transsylvanica*, Benedek *et al.* (2011) assume a maximum distance of 250 m for regular dispersal among patches in a meta-population, based on data for a related species from the same genus, *P. griseoptera* presented by Diekotter *et al.* (2005). This is in line with results for another wingless bush cricket, *Metrioptera bicolor* (Kindvall 2002). We therefore assume 250 m as a likely maximum for genetic exchange in members of this family.

*Myrmecophilus baronii*, as a member of the family of ant-loving crickets (Myrmecophilidae), has a very particular ecology and distribution. They are found inside the nests of a limited number of host ant species, and their habitat is restricted to sparsely vegetated grasslands in which nests of these ant species occur. The species is small and flightless, and likely has a very limited dispersal capacity, although no data are available so far.

The grassland-related grasshoppers listed on the Habitats Directive are all members of the large family *Acrididae*, which are extremely variable in wing and body size, and include flying as well as flightless species. Most research on dispersal of Acrididae relates to a subset of species known as locusts, which show swarming behaviour in groups and can migrate over hundreds of kilometers, and are major pests in agricultural fields. Yet, none of the Acrididae in the current species set are locusts, and all but one are wingless, likely showing similar dispersal distances as the bush crickets. For the only flying species, *Stenobothrus eurasius*, no data are available so far. Two members of the same genus included in the list of Reinhardt *et al.* (2005) are classified in the 'low mobility' class 1, suggesting that dispersal distance in this genus is likely also restricted to a few hundred meters.

### **3.2.3 Coleoptera**

Available knowledge for coleoptera strongly differs per taxon. Multiple experimental studies have been conducted for the stag beetle (*Lucanus cervus*), a well-known emblematic species with a relatively large distribution range. Data for this species are of high quality, as its body size allowed the use of radio transmitters for detailed study of dispersal trajectories of individual beetles. For some species, including two carabids and two cerambycids, a MRR study provided some insight, although in most cases data were based on a relatively limited study area and/or sample size, resulting in a potential underestimation of long-distance dispersal. This may have resulted in an underestimation of dispersal rates especially for *Osmoderma eremita* and hampered estimation of long-distance dispersal in this species (Ranius & Hedin 2001). Yet, (long-distance) dispersal is likely indeed rare in this very sedentary species and may only result in effective gene flow and colonization for larger source populations (Ranius & Hedin 2001).

All four carabids are wingless, resulting in relatively limited dispersal ranges, although most species are rapid runners that seem capable of crossing e.g. arable fields of at least 250 m wide. Long-distance dispersal up to 1km has been reported for *Carabus hungaricus* (Elek *et al.* 2014) and is likely similar for the other carabids. Little is known about dispersal barriers. Little data are available for various other species with varying morphology and ecology, limiting possibilities for extrapolation of dispersal capacities.

### 3.2.4 *Lepidoptera*

A large amount of studies is available on dispersal capacities of butterflies and moths. Nevertheless, much is still unknown. This is caused both by the vast number of species in this order and by a wide variation among them in morphology and life history resulting in large variation in dispersal behaviour, limiting possibilities to generalize among ecological or taxonomic groups. Dispersal ranges vary from tens of meters to tens of kilometers. For several species, again both in butterflies and moths, differences in dispersal capacity exist between sexes, with males showing somewhat higher dispersal distances than females.

Given the overall abundance of papers on especially butterfly ecology, surprisingly little knowledge is available on the potential limiting effects of natural or human-made landscape elements on their dispersal. For most species, waterways are unlikely to be a barrier, with the exception of the females of two of the geometrid species with flightless females. Effects of roads are virtually unknown. More research in this respect is urgently needed, especially in case road verges are considered as valuable habitat for improvement of landscape connectivity (see 3.3.4).

### 3.2.5 *Mantodea*

Published knowledge on dispersal capacities of Mantodea is extremely limited and restricted to broad statements based on the presence of functional wings. While all juveniles are wingless, mantid taxa can be grouped based on the wings present in adult individuals, being either macropterous (long-winged), brachypterous (short-winged), micropterous (vestigial-winged), or apterous (wingless) (Roy 1999). The only mantid species included in the current species list is *Apteromantis aptera*, which is (as indicated by its name) and apterous species. This likely inhibits dispersal across waterways and potentially limits its dispersal across larger roads. The species is reported to jump agilely, which may to some extent compensate for its inability to fly. Yet, no evidence is so far available on its potential to cross roads. In fact, any information on dispersal distances for this species is limited to one source stating a 'low dispersal capacity' (Boieiro *et al.* 2007).

## 3.3 Potential measures for improvement of connectivity

### 3.3.1 *Odonata*

Our results (Annex 2) show that while Odonata in general seem quite mobile, colonization distances may vary widely even among congeneric species, as exemplified by the most intensively studied damselfly genus *Coenagrion*. Some species may successfully colonize sites at >25 km distance, while for others this range is likely limited to 1-2 km. For many Anisoptera there is a clear lack of information, although a dispersal range of at least >1 km seems likely.

Yet, while this suggests that for recolonization corridors may hardly be needed, in practice especially many damselflies strictly follow the shoreline vegetation along lakes or rivers, and may only disperse into terrestrial habitats (grassland, woods) for a few hundred meters. Moreover, in both species of damselflies and dragonflies, MRR experiments suggest dispersal to be rather limited for the vast majority of individuals, with individuals not regularly moving away more than a few hundred meters from their breeding habitat. As estimations of gene flow are so far rarely available, it remains unknown whether occasional long-distance dispersal is common enough to avoid genetic erosion. Especially for small populations this may not be the case. All in all, corridors are advised, and should consist of at least stepping stones for dragonflies (located maximum 500 m apart). For damselflies stepping stones (located maximum 300 m) are ideally connected via shoreline vegetation.

### 3.3.2 Orthoptera

Colonization distances are hardly known for the studied Orthopteran species and any advices on connectivity have to rely on data from MRR studies. Based also on the apterous ecology of most species involved, this results for the moment in rather conservative connectivity estimates assuming little or no dispersal over more than 250 m. Therefore line-shaped grassland corridors seem a logical conclusion for this species group.

### 3.3.3 Coleoptera

Given their short dispersal distances, line-shaped corridors are likely optimal for the wingless species, including at least the Carabidae as well as *Dorcarion fulvum cervae* and *Probaticus subrugosus*. Species seem able to cross one to several hundreds of meters of unsuitable habitat, including intensive agricultural fields (arable land; Torres-Villa *et al.* 2017, Baur *et al.* 2005), suggesting that occasional gaps between corridors of at least 100 m can be bridged. Optimal structure of such line-shaped habitats differs between species. Most of the typical grassland species may be able to make use of road verges some mainly following tree lines while others appear able to follow road verges.

The flying species at least need a stepping stone type corridor. Optimal habitat structure of the stepping stones varies between species, with some species requiring specific additional elements to complete their life cycle. Examples are *Cerambyx cerdo*, *Osmoderma eremita* and *Lucanus cervus*, requiring open woodland or at least solitary old trees for sustainable provision of breeding habitat. Based on current (limited) knowledge, maximum distances between breeding habitats should not exceed 1 km to allow successful recolonization, while genetic exchange between distance patches may require stepping stones in between that are maximum 200 to 500 m apart. A corridor of the nodal type, in which the abovementioned stepping stones are connected by grassland vegetation, may ease dispersal (see Van der Sluis & Bouwma 2018 for a more detailed description of habitat needs).

### 3.3.4 Lepidoptera

The Lepidoptera show strong differences in dispersal distances and therefore in needs for corridors. At one extreme, the butterflies of the genus *Zerynthia* and the moth *Euplagia quadripunctaria* can occasionally bridge >10 km for colonization of distant patches, while regularly dispersing over multiple kilometers. These species likely already benefit from a mosaic of habitat fragments across the landscape and may not need specific fine-scale corridor measures. At the other extreme, for *Parnassius mnemosyne* dispersal over a few hundred meters was already reported to take multiple years and will likely require more or less continuous stretches of habitat. For this species, linear corridors consisting of flower-rich grassland may thus be ideal.

A gradient of intermediate dispersal capacities occurs both among the butterflies and among the moths. Some species, with dispersal ranges of multiple kilometers, may benefit especially from a landscape with a mosaic of habitat fragments that can be one or a few kilometers apart. Longer distances may be bridged by supplying small habitat patches that mainly provide sufficient flower availability for foraging, to restock for a next flight. Other species, with dispersal ranges of a few hundred meters or less, may require linear corridors consisting of flower-rich grassland. Road verges can play an important role in this respect for a wide range of Lepidoptera when managed properly to sustain sufficient flowers (see e.g. Saarinen *et al.* 2005).

### 3.3.5 Mantodea

Given its very limited dispersal, Apteromantis aptera will likely need near continuous habitat for dispersal, and will benefit from corridors consisting of linear grassland elements.

## 4 Discussion and further study

Maximum dispersal distances provide an upper limit for distance between habitat patches to ensure effective connectivity. As the amount of dispersal events depends on population size, maximum distances will be realized only rarely in case of sufficiently large population sizes. Thus, while maximum distances may ensure connectivity in case of relatively large and high-quality habitat patches, distances are ideally reduced in cases of strong habitat fragmentation or for species intrinsically occurring in very low densities and/or very patchy distributions.

In the current study, for various species of grassland arthropods listed on the Habitat Directive's annexes, we were able to retrieve at least data on maximum dispersal distances based on mark-release-recapture (MRR) studies. While this gives an indication of dispersal abilities for trans-habitat movement, it likely underestimates long-distance dispersal. (Re)colonization of suitable patches may often occur over larger distances, yet quantitative estimates of maximum long-distance dispersal distances so far strongly rely on anecdotal evidence. Whether the observed maxima are realized often enough to allow gene flow to an extent that successfully limits genetic erosion mostly remains unsure and, again, also depends on population size. Therefore, we here took a conservative approach and based connectivity needs for genetic exchange on the distance range within which 95 % of the individuals dispersed as estimated from MRR-based dispersal kernels.

Although more data are available for several of the orders included in this study, data availability is rather limited for the current set of study species within those orders, which are mostly relatively rare and restricted to a limited distribution area. Strong variation in life history and feeding and breeding ecology currently limited our abilities to extrapolate dispersal ranges among species. Yet, several studies report relations of average dispersal capacity with either phylogeny, morphological traits or ecological traits, which yields potential to estimate dispersal capacities for more species without performing extensive experimental studies for each of them. Relations with wing span may be promising in this respect, as such data are available even for rarely studied species. Yet, reliable extrapolation will depend on further quantification of this relationship.

Especially for the Orthoptera, Mantodea and to some extent Coleoptera protected via the Habitats Directive, more data collection on dispersal abilities is urgently needed to inform more precise recommendations on corridor needs and to allow the modelling of landscape-scale connectivity via e.g. LARCH (Van der Sluis *et al.* 2007). Ideally such studies should combine MRR with analysis of inter-population gene flow and estimation of population size, which can be realized by using DNA-based mark-recapture approaches (see e.g. Epopa *et al.* 2017). Furthermore, studies should comprise a set of populations with a broad range in pairwise geographic distances and varying population sizes.

Knowledge on the relevance of infrastructural elements as dispersal barriers is even less existent. While over the last decade the field of road ecology has been explored rather extensively for vertebrates, only few example studies are available for insects. A review of those examples by Munoz *et al.* (2015) concluded that roads may be major barriers for especially small and wingless insects. Yet, studies on vertebrates have shown clear differences among species and the same may be true for insects. Alternative movement strategies, such as the ability to jump in orthopterans, as well as road type (width, type of material, traffic volumes) will strongly influence both mortality rates when crossing and willingness of the species to cross or live near the road (Munoz *et al.* 2015). More knowledge on road ecology for protected arthropods is required, with special emphasis on the wingless species.

The current study provides a proof-of-principle for connectivity needs of a specific subset of protected arthropods, i.e. those related to grassland habitats. As input for connectivity measures in the context of TEN-N, a similar knowledge basis will also be needed for arthropods depending on different habitat types, such as scrublands, forests or wetlands.

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# Annex 1 Species selection

Table S1: List of species included in the analyses presented in this report, selected based on 1) occurrence on either Annex II or IV of the Habitats Directive and 2) relation with grassland habitats (including semi-natural pastures, xerotherm and steppe grasslands).

order LAT	Suborder LAT	Suborder EN	Family LAT	Family EN	Species name
Odonata	Zygoptera	Damselflies	Coenagrionidae	pond damselflies	<i>Coenagrion hylas</i>
Odonata	Zygoptera	Damselflies	Coenagrionidae	pond damselflies	<i>Coenagrion mercuriale</i>
Odonata	Zygoptera	Damselflies	Coenagrionidae	pond damselflies	<i>Coenagrion ornatum</i>
Odonata	Zygoptera	Damselflies	Lestidae	spread-winged damselflies	<i>Sympecma paedisca</i>
Odonata	Anisoptera	Dragonflies	Corduliidae	emerald dragonflies	<i>Macromia splendens</i>
Odonata	Anisoptera	Dragonflies	Corduliidae	emerald dragonflies	<i>Oxygastra curtisii</i>
Odonata	Anisoptera	Dragonflies	Gomphidae	club-tailed dragonflies	<i>Lindenia tetraphylla</i>
Odonata	Anisoptera	Dragonflies	Gomphidae	club-tailed dragonflies	<i>Ophiogomphus cecilia</i>
Odonata	Anisoptera	Dragonflies	Gomphidae	club-tailed dragonflies	<i>Stylurus flavipes</i>
Odonata	Anisoptera	Dragonflies	Libellulidae	skimmers	<i>Leucorrhinia pectoralis</i>
Orthoptera	Ensifera	crickets	Myrmecophilidae	ant-loving crickets	<i>Myrmecophilus baronii</i>
Orthoptera	Ensifera	crickets	Tettigoniidae	bush crickets	<i>Baetica ustulata</i>
Orthoptera	Ensifera	crickets	Tettigoniidae	bush crickets	<i>Isophya costata</i>
Orthoptera	Ensifera	crickets	Tettigoniidae	bush crickets	<i>Isophya harzi</i>
Orthoptera	Ensifera	crickets	Tettigoniidae	bush crickets	<i>Isophya stysi</i>
Orthoptera	Ensifera	crickets	Tettigoniidae	bush crickets	<i>Pholidoptera transsylvanica</i>
Orthoptera	Ensifera	crickets	Tettigoniidae	bush crickets	<i>Saga pedo</i>
Orthoptera	Caelifera	grasshoppers	Acrididae	NA	<i>Odontopodisma rubripes</i>
Orthoptera	Caelifera	grasshoppers	Acrididae	NA	<i>Paracaloptenus caloptenoides</i>
Orthoptera	Caelifera	grasshoppers	Acrididae	NA	<i>Stenobothrus eurasius</i>
Coleoptera	Adephaga	NA	Carabidae	ground beetles	<i>Carabus hampei</i>
Coleoptera	Adephaga	NA	Carabidae	ground beetles	<i>Carabus hungaricus</i>
Coleoptera	Adephaga	NA	Carabidae	ground beetles	<i>Carabus variolosus</i>
Coleoptera	Adephaga	NA	Carabidae	ground beetles	<i>Carabus zawadzki</i>
Coleoptera	Phytophaga	NA	Cerambycidae	longhorn beetles	<i>Cerambyx cerdo</i>
Coleoptera	Phytophaga	NA	Cerambycidae	longhorn beetles	<i>Dorcadion fulvum cervae</i>
Coleoptera	Phytophaga	NA	Cerambycidae	longhorn beetles	<i>Pilemia tigrina</i>
Coleoptera	Phytophaga	NA	Cerambycidae	longhorn beetles	<i>Pseudogaurotina excellens</i>
Coleoptera	Polyphaga	NA	Geotrupidae	dung beetles	<i>Bolbelasmus unicornis</i>
Coleoptera	Polyphaga	NA	Scarabaeidae	scarab beetles	<i>Osmoderma eremita</i> complex
Coleoptera	Polyphaga	NA	Lucanidae	stag beetles	<i>Lucanus cervus</i>
Coleoptera	Polyphaga	NA	Tenebrionidae	darkling beetles	<i>Probaticus subrugosus</i>
Lepidoptera	Rhopalocera	Butterflies	Hesperiidae	skippers	<i>Hesperia comma catena</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Agriades glandon aquilo</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Lycaena dispar</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Lycaena helle</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Maculinea arion</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Maculinea nausithous</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Maculinea teleius</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Plebicula golgus</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Polyommatus eroides</i>
Lepidoptera	Rhopalocera	Butterflies	Lycaenidae	gossamer-winged butterflies	<i>Pseudophilotes bavius</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Clossiana improba</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Coenonympha hero</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Coenonympha oedippus</i>

Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Erebia calcaria</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Erebia christi</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Erebia medusa polaris</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Erebia sudetica</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Euphydryas aurinia</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Euphydryas maturna</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Fabriciana elisa</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Melanargia arge</i>
Lepidoptera	Rhopalocera	Butterflies	Nymphalidae	brush-footed butterflies	<i>Proterebia afra dalmata</i>
Lepidoptera	Rhopalocera	Butterflies	Papilionidae	Swallowtail butterflies	<i>Papilio alexanor</i>
Lepidoptera	Rhopalocera	Butterflies	Papilionidae	Swallowtail butterflies	<i>Papilio hospiton</i>
Lepidoptera	Rhopalocera	Butterflies	Papilionidae	Swallowtail butterflies	<i>Parnassius apollo</i>
Lepidoptera	Rhopalocera	Butterflies	Papilionidae	Swallowtail butterflies	<i>Parnassius mnemosyne</i>
Lepidoptera	Rhopalocera	Butterflies	Papilionidae	Swallowtail butterflies	<i>Zerynthia cassandra</i>
Lepidoptera	Rhopalocera	Butterflies	Papilionidae	Swallowtail butterflies	<i>Zerynthia polyxena</i>
Lepidoptera	Rhopalocera	Butterflies	Pieridae	NA	<i>Colias myrmidone</i>
Lepidoptera	Rhopalocera	Butterflies	Pieridae	NA	<i>Leptidea morsei</i>
Lepidoptera	Heterocera	Moths	Cossidae	Carpenter millers	<i>Catopta thrips</i>
Lepidoptera	Heterocera	Moths	Erebidae	Erebid moths	<i>Euplagia quadripunctaria</i>
Lepidoptera	Heterocera	Moths	Geometridae	Geometer moths	<i>Chondrosoma fiduciarium</i>
Lepidoptera	Heterocera	Moths	Geometridae	Geometer moths	<i>Lignyopectera fumidaria</i>
Lepidoptera	Heterocera	Moths	Geometridae	Geometer moths	<i>Phyllometra culminaria</i>
Lepidoptera	Heterocera	Moths	Glyphipterigidae	Sedge moths	<i>Glyphipterix loricatella</i>
Lepidoptera	Heterocera	Moths	Lasiocampidae	Snout moths	<i>Eriogaster catax</i>
Lepidoptera	Heterocera	Moths	Noctuidae	Owlet moths	<i>Arytrura musculus</i>
Lepidoptera	Heterocera	Moths	Noctuidae	Owlet moths	<i>Cucullia mixta</i>
Lepidoptera	Heterocera	Moths	Noctuidae	Owlet moths	<i>Gortyna borelii lunata</i>
Lepidoptera	Heterocera	Moths	Noctuidae	Owlet moths	<i>Polymixis rufocincta isolata</i>
Lepidoptera	Heterocera	Moths	Sphingidae	Sphinx moths	<i>Proserpinus proserpina</i>
Mantodea	NA	NA	Amelidae	NA	<i>Ateromantis aptera</i>

## **Annex 2 Database of dispersal capacities and habitat dependencies per species**

Tables per arthropod order were compiled in an excel database available as a separate file:

**Arthropod connectivity tables\_v1.0.xlsx**